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PULVINAR'S ROLE IN INFORMATION TRANSMISSION THROUGH THE VISUAL CORTICAL HIERARCHY

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ABSTRACT

A hierarchical model of ten cortical areas is examined to explain representation of stimulus contrast. In each area, the activity is integrated and then non-linearly transmitted to the next area. This arrangement of interactions creates a gradient from simple to complex visual patterns as one moves to higher cortical levels. In the model, the firing rate of each unit describes its neural activity. The visual input is modeled as a Gaussian random input, whose width codes for the contrast. This input is applied to the first area. The output activity ratio among different contrast values is analyzed for the last level to observe sensitivity to a contrast and contrast invariant tuning. For a purely cortical system, the output in the last area is approximately contrast invariance in a small gain range, but the sensitivity to contrast is poor. To account for an alternative visual processing pathway, non-reciprocal connections from and to a parallel pulvinar like-structure of nine areas are coupled to the system. Compared to the pure feedforward model, cortico-pulvinar-cortical output presents much more sensitivity to contrast and has a similar level of contrast invariance of the tuning.

KEY WORDS

Biophysical models, Cortical transmission, Cortico-pulvinar connections, Sensitivity to Contrast, Tuning Contrast Invariance.

1 Introduction

The primate visual system is a highly complex structure with a hierarchical organization of areas [1]. In this hierarchy, feedforward connections are almost exclusively from areas in one layer to areas in the next layer of the hierarchy, while the feedback connections are predominantly to areas in the preceding layer. If we investigate the response properties for neurons in higher and higher layers of the hierarchy, several features are striking. The receptive fields of the neurons increase in size and become more complex [2]. Nevertheless the tuning properties of the neurons are more or less contrast invariance and the response increases smoothly with contrast [3].

These properties are not easily accounted for. Simple

models show that, because to the non-linear input-output relation of the neurons, chains of areas will develop the tendency to move to a step response, or go to a constant response as a function of contrast [4].

What seems to be needed to overcome this problem is a “short-cut” between lower and higher layers in the hierarchy. A candidate for such a short-cut is the pulvinar nucleus of the thalamus [5]. The pulvinar is hierarchically organized [6], but unlike the cortex pulvinar layers are connected by long range interneurons [7]. Furthermore there is a topological arrangement of connectivity between pulvinar and the cortex that conserves the topography of the visual system [5, 6]. Thus, the pulvinar can transmit topographical visual information from lower cortical areas to higher levels by long range interneurons.

Here we investigate whether the pulvinar can play an important role in regulating the response of higher cortical areas to contrast changes. We investigate a toy model of the visual cortex with and without interactions with the pulvinar and study in both cases to what extend it is possible to have contrast independent tuning and a smooth contrast response function in all layers of the hierarchy.

2 The Model

We consider a network model with a hierarchical cortical architecture. It consists of L areas, with in each area 2^L different units. The units are modeled as rate based neurons [8]. Beside this cortical architecture there is also a model pulvinar with $L - 1$ layers, whose units are also modeled as rate based neurons.

The Transfer Function

Each unit is considered as being composed of “On” and “Off” cells, where the rates r_+ of the “On” and r_- of the “Off” cells satisfy, if the input into the unit is I ,

$$\tau_r \frac{d}{dt} r_{\pm} = -r_{\pm} + f_{\pm}(I) \quad (1)$$

where τ_r is the time constant of the cortical units and f_{\pm} are sigmoidal functions, satisfying $f_{+}(I) = [1 + \exp(-\beta(\pm I - I_{th}))]^{-1}$. The “On” and “Off” units can

be combined in one effective unit with a rate $r = r_+ - r_-$, which has a transfer function

$$f(I) = \frac{1}{1 + \exp(-\beta(I - I_{th}))} - \frac{1}{1 + \exp(\beta(I + I_{th}))}. \quad (2)$$

The rate of the units in the pulvinar obey the same dynamics.

Cortical Architecture

The input onto a cortical unit in area l has three components, cortical feedforward input from area $l - 1$, cortical feedback from $l + 1$ and pulvinar input from pulvinar area $l - 1$. The exception to this are the first area which receives feedforward input from the LGN and feedback from cortical area 2, but not from the pulvinar, and the last area, area L , which does not receive cortical feedback input.

We account for the increasing size and complexity of the receptive field as one moves up the cortical hierarchy by assuming that in each area the units receive input from two neighboring units in area $l - 1$. For example, at position i in area 2 there are two units, one which receives as input the sum of the outputs of position $2i - 1$ and $2i$ in area 1, while the other receives the difference of these outputs. Thus we have half as many positions in area 2, but two types of neurons in each position. This procedure is repeated in higher areas. Thus for unit i of type k in cortical area l the feedforward input, $I_{k,i}^l(FF)$ satisfies

$$\begin{aligned} I_{2k-1,i}^l(FF) &= r_{k,2i-1}^{l-1} + r_{k,2i}^{l-1} \\ I_{2k,i}^l(FF) &= r_{k,2i-1}^{l-1} - r_{k,2i}^{l-1}, \end{aligned} \quad (3)$$

for $l = 2, \dots, L - 1, i = 1, \dots, 2^{L-l}$ and $k = 1, \dots, 2^{l-1}$. For $l = 1$ we have only one type of receptive field, $k = 1$ and $I_{1,l}^1(FF)$ is, for $i = 1, \dots, 2^{L-1}$, given by $I_{1,l}^1(FF) = r_i^0$, where r_i^0 is the output of the i th LGN unit.

Units in area l receive feedback input from those units in area $l + 1$ in to which they project, this input has the same sign as the feedforward input but is modulated by factor γ . The feedback is given by

$$\begin{aligned} I_{k,2i-1}^l(FB) &= \gamma(r_{2k-1,i}^{l+1} + r_{2k,i}^{l+1}) \\ I_{k,2i}^l(FB) &= \gamma(r_{2k-1,i}^{l+1} - r_{2k,i}^{l+1}). \end{aligned} \quad (4)$$

Units on the L th area do not receive feedback input. To account for the absence of this we for this area that the feedforward input is given by $I_{2k-1,1}^L(FF) = (1 + \gamma)[r_{k,1}^{L-1} + r_{k,2}^{L-1}]$ and $I_{2k,1}^L(FF) = (1 + \gamma)[r_{k,1}^{L-1} - r_{k,2}^{L-1}]$.

The Pulvinar

The pulvinar is modeled similarly to the cortex except that each area has at most 4 types of receptive fields, the patterns corresponding to $k = 1, 2, 2^l - 1, 2^l$. Pulvinar units in area l receive input from cortical units in area l and from pulvinar units in areas 1 to $L - 1$. The input

$J_{k,i}^l(PC)$ from cortex to unit i of type k in pulvinar region l is given by $J_{k,i}^l(PC) = W_{PC}I$ for $l = 1, \dots, L - 1, i = 1, \dots, 2^{L-l-1}$ and $k = 1, 2, 2^l - 1, 2^l$. The input $J_{k,i}^l(PP)$ from the rest of the pulvinar satisfies:

$$\begin{aligned} J_{2k-1,i}^l(PP) &= \frac{1}{1 + W_{LP}} \left(W_{FP}[s_{k,2i-1}^{l-1} + s_{k,2i}^{l-1}] \right. \\ &\quad \left. + \frac{W_{LP}}{2}[J_{k,2i-1}^{l-1} + J_{k,2i}^{l-1}] \right) \\ J_{2k,i}^l(PP) &= \frac{1}{1 + W_{LP}} \left(W_{FP}[s_{k,2i-1}^{l-1} - s_{k,2i}^{l-1}] \right. \\ &\quad \left. + \frac{W_{LP}}{2}[J_{k,2i-1}^{l-1} + J_{k,2i}^{l-1}] \right), \end{aligned} \quad (5)$$

for $k = 1$ and $k = 2^{l-1}$. Here we have used $s_{k,i}^l$ for the rate of the pulvinar units and assumed $J_{k,i}^1(PP) = 0$. Variables W_{FP} and W_{LP} are respectively strengths that modulate the feedforward and the long range forward input inside the pulvinar, and they can be positives or negatives. The exception to this connectivity arrangement are pulvinar area 1 and 2. Pulvinar area 1 receives only input from cortical area 1, whereas for pulvinar area 2 $W_{LP} = 0$.

Finally, the input from pulvinar to cortex, $I(CP)$, is given by:

$$\begin{aligned} I_{2k-1,i}^l(CP) &= W_{CP}[s_{k,2i-1}^{l+1} + s_{k,2i}^{l+1}] \\ I_{2k,i}^l(CP) &= W_{CP}[s_{k,2i-1}^{l+1} - s_{k,2i}^{l+1}], \end{aligned} \quad (6)$$

where $s_{k,i}^l$ is the output of pulvinar unit for $k = 1, 2, 2^l - 1, 2^l$ and $s_{k,i}^l = 0$ otherwise.

3 Response to Homogeneous Input

To get some insight into the model's behavior we first consider the network with a spatially constant input, $r_i^0 = r_0$. For such an input the equilibrium rates satisfy $r_{k,i}^l = \delta_{k,1}r_l, s_{k,i}^l = \delta_{k,1}s_l$.

In the purely feedforward model, $\gamma = 0$ and $W_{CP} = 0$ these rates are given by $r_1 = f(r_0), r_{l+1} = f(2r_l)$. If we consider a long chain, L large, the rates will approach r_∞ , given by $r_\infty = f(2r_\infty)$. Figure 1A shows the solutions for r_∞ as a function of β . For small β the only solution is $r_\infty = 0$. As β is increased there is a bifurcation and two new solutions appear. The solution $r_\infty = 0$ becomes unstable at this point while the two new solutions are stable.

The meaning of these results is that for small β the response, r_l , approaches 0 with increasing l for any input r_0 , while for large β it approaches upper stable solution for $r_0 > 0$ and the lower one for $r_0 < 0$. Thus information about r_0 is lost in the higher areas for any value of β .

Adding feedback connections only, $\gamma \neq 0, W_{CP} = 0$ does not qualitatively improve the situation. The bifurcation point moves from $\beta_{cr} = 1$ to $\beta_{cr} = 2/(2 + \gamma)$, but for a sufficiently large L we still have an almost constant output for small β and a step response for larger β .

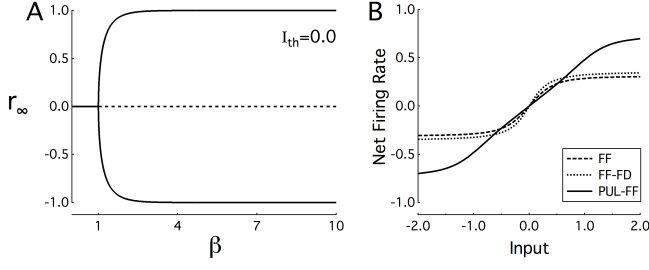


Figure 1. A) Fixed point solutions as a function of β . Solid: stable, dashed: unstable. B) Response of the 10th layer as a function of input for the optimal feedforward (FF), feedforward-feedback (FF-FD) and pulvinar-feedforward (PUL-FF) network.

The response of the network to spatially constant input with the pulvinar included, $W_{CP} \neq 0$ and $W_{PC} \neq 0$, can also be treated analytically. One solution shows a smooth linear increment of firing rate when the contrast input gradually increases. This relation in the feedforward-pulvinar model is observed when $W_{LP} \gg 1$ with the constraint $W_{FP} < W_{LP}$. At $I_{th}^{cx} = 0$, this process is satisfied as $\beta^{cx} = 1/(1 + F_{pul}W_{CP}W_{PC})$, where β^{cx} is the cortical gain and F_{pul} the derivative of the effective transfer function for the pulvinar (Eq. (2)). This improvement in the last area's activity is because pulvinar area l receives input from all lower areas and passes directly to higher areas. Because of these long range interactions, responses in the higher pulvinar regions may not tend to a bi-modal output distribution. This is confirmed by numerical simulations. These show that the output of the last layer increases much more smoothly when the pulvinar is included.

A network that optimally encodes r_0 in the final layer should satisfy two requirements, It should be as linear as possible and it should use the output range maximally. For a cortical feedforward network these requirements are in conflict. The dynamic range is used maximally for large β , but for large β the response is very non-linear. On the other hand small β give an almost linear response, but the output does not use the dynamic range. Figure 1B shows the output of the last area for a network that optimally encodes inputs, r_0 between -2 and 2. The optimality measure used was the entropy of the output distribution and the value of β was optimized (I_{th} was kept at 0). The input output function is far from linear and the range $[-1, 1]$ is not fully used. Also shown is the result for feedforward-feedback and feedforward-pulvinar model. Here $\beta^{cx, pul}$, γ , W_{CP} , W_{PC} , W_{FP} and W_{LP} were varied to obtain the optimal value. For PUL-FF model, β^{cx} was found to satisfy using $\beta^{cx} = 1/(1 + F_{pul}W_{CP}W_{PC})$. The result for PUL-FF is much better than that for cortico-cortical connections. The curve is closer to linear and the dynamical range is almost fully used. In this simple set-up the pulvinar can contribute greatly to the transmission of information about the input to the highest layer.

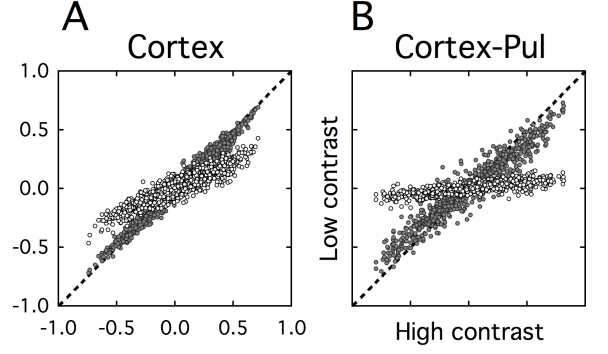


Figure 2. Scatter-plot of response at low contrast (White dots $\sigma^2 = 0.1$, gray dots $\sigma^2 = 0.5$) vs. response at the highest contrast ($\sigma^2 = 1$) that minimize the error. A) Feedforward network, B) Network with pulvinar.

4 Response to Visual Input

In modeling the response of the network to Natural Visual stimuli we take into account that for such stimuli the retina and LGN whitens the response and reduces the kurtosis of the distribution [9]. Thus visual input with natural statistics is, in our model, described by a random input with mean 0, $r_i^0 = \sigma x_i$, where σ codes for the contrast and x_i is independently drawn from a Gaussian with mean 0 and variance 1. We assume that the same visual input with higher contrast is represented by an input with the same x_i but larger σ . Contrast invariance of the tuning means that the input elicits in the last layer an output vector $r_{k,1}^L$ whose direction is independent of contrast. Smooth increase of the contrast response means that the length of this vector increases gradually with contrast.

If we consider a purely feedforward model in which the transfer function f is linear, $f(I) = \alpha I$, the output of each layer is Gaussian and one easily shows $\langle (r_{k,i}^L)^2 \rangle = (2\alpha^2)^l \sigma^2 / 2$. The response decreases with l if $\alpha < \alpha_{cr} = 1/\sqrt{2}$, otherwise it blows up.

Considering a feedforward network with a nonlinear transfer function, f , we see that, for low contrast, the response goes to zero if $f'(0) < \alpha_{cr}$. For $I_{th} = 0$ this means that $\beta = \sqrt{2}$. Applying a Gaussian random input r^0 generates, for $I_{th} = 0$, in layer L , one or three fixed rate bumps, as one moves from small to large values of β . Firing rates pass from $r^L = 0$ to $r^L = -1, 0, 1$ as β is increased. These solutions are produced for inputs with low and high contrast. Numerical simulation shows that the transition from one bump to three bumps occurs at $\beta \approx 1.4$, in agreement with our analysis.

5 Output Response Tuning

To test whether the network is sensitive to changes in contrast, we measure the output activity of the last layer when

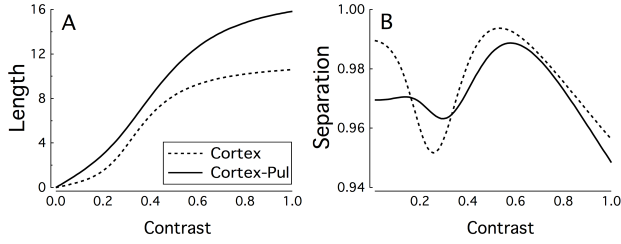


Figure 3. A) Length and B) Separation distance of last area outputs as a function of contrast.

the variance, σ^2 , is gradually increased. We estimate two properties of the output firing rate: The output amplitude is a function of the contrast and the mean angle between different values of contrast. The output amplitude, F , is defined as average length of the output for LGN inputs with widths σ , $F(\sigma) = \langle |\vec{V}| \rangle$, where the average is over input patterns with standard deviation σ . We aim for an amplitude function F that is as linear as possible and uses the dynamic range maximally. We use E_L defined as $E_L = -\int_0^1 d\sigma \log(F'(\sigma))$ as the cost-function for this property. $E_L \rightarrow 0$ the output scales linearly and exploits the whole dynamic ranges. It increases if less of the dynamic range is used or the response is more non-linear. To explore whether the network can maintain contrast invariant tuning, we calculate the mean of the separation distance S between normalized output vectors $\vec{e}(\sigma)$ and $\vec{e}(\sigma')$ for LGN inputs $r_i^0 = \sigma x_k$ and $r_i^0 = \sigma' x_k$ respectively, $S = \int_0^1 d\sigma \int_0^1 d\sigma' \vec{e}(\sigma) \cdot \vec{e}(\sigma')$. Here $\vec{e} = \vec{V}/\|\vec{V}\|$. If $S = 1$ then vectors are in the same direction for all contrasts. As the direction changes more with contrast, S decreases. We define an error $E = \frac{5}{2}S + e^{-E_L}$ that takes both these factors into account.

For networks with different architectures we determine the parameters which minimize the cost function E . In Fig. 2 we show the response to different contrast for a model with only intracortical feedforward connections (Fig 2A) and with the complete Cortex + Pulvinar System (Fig 2B). The response of a neuron at contrast σ is plotted against the response of the same cell at contrast $\sigma = 1$ for different values of the contrast. For both architectures the contrast invariance of the tuning reasonable good, as reflected by the fact that the points fall nearly on a straight line. However, for the feedforward model, the slope of this line does not change much as σ is varied, reflecting the fact that the response amplitude only changes weakly with the contrast. Furthermore the dynamic range is not fully used here.

In the cortico-pulvinar-cortical model the dynamical range is almost fully exploited and the response amplitude increases by almost a factor of 5 as the contrast is increased from $\sigma^2 = 0.1$ to $\sigma^2 = 1$. This is further illustrated in Fig. 3. In Fig 3A we plot the average response amplitude against the contrast for both architectures and in Fig. 3B the sepa-

ration between the normalized response vector for contrast σ and the normalized response vector averaged over contrasts, is plotted against σ . For both models S varies over the range 0.99 to 0.94, but the response amplitude clearly increases more linearly and uses more of the dynamic range for the Cortico-pulvinar-cortex model.

This improvement is observed as $W_{LP} \gg 1$ and $W_{FP} < W_{LP}$. Moreover, this improvement is present when connections from cortex to pulvinar are negative (positive) while connections from pulvinar to cortex are positive (negative). Surprisingly there are two almost equally good solutions: in one W_{CP} is large and W_{PC} small. In the other W_{PC} is large and W_{CP} small. Our model does well when the cortex modulates the pulvinar while the pulvinar drives the cortex, but it does equally well when it is the other way around.

These results show that in a purely feedforward model it is not possible to achieve contrast independent tuning and a good sensitivity to contrast in higher layers of the visual hierarchy and that the pathway through the pulvinar could overcome this limitation.

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